



How to classify forests? A case study from Central Europe

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Abstract

Aims: Inconsistent treatment of the vegetation layers is one of the main problems in the floristic classification of forests. In this study I investigate whether a classification based solely on woody species leads to units similar to the Braun-Blanquet system or to something completely different. **Study area:** Austria (Central Europe) and adjacent regions. **Methods:** 23,681 forest relevés from the Austrian Vegetation Database were classified using TWINSpan. Spruce and pine plantations and stands with a cover of non-native woody species > 5% were excluded from the dataset. Only native tree and shrub species were used in the classification while herbs, dwarf shrubs, cryptogams and all records of woody species in the herb layer were omitted. **Results:** The TWINSpan classification revealed elevation (i.e., climate) as the main floristic gradient in the data set. Within lowland communities, soil moisture was the dominant factor. The higher units of the Braun-Blanquet system were mostly well reproduced. **Conclusions:** The higher levels of the phytosociological forest classification (class, order, partly also alliance) can basically be defined by taking only the shrub and tree layer into account. However, all past and current classifications suffer from arbitrary exceptions to this rule. This leads to many inconsistencies and blurs the main biogeographical patterns within European forests. Here I argue that using the tree and shrub species for defining the higher levels and the understorey species for defining the lower ones is best suited to meet the properties that users would expect from a good forest classification.

Taxonomic reference: Fischer et al. (2008).

Syntaxonomic reference: Mucina et al. (2016) if not stated otherwise.

Abbreviations: EVC = EuroVegChecklist (Mucina et al. 2016).

Keywords

Braun-Blanquet approach, forest, shrub layer, tree layer, vegetation classification

Introduction

The classes of the Braun-Blanquet system correspond to major floristic, biogeographical and ecological units (Pignatti et al. 1995; Loidi 2020). For European zonal forests, these are the *Quercetea ilicis* (mediterranean evergreen), *Quercetea pubescentis* (submediterranean deciduous), *Quercetea robori-petraeae* and *Carpino-Fagetea*

(temperate deciduous), *Vaccinio-Piceetea* (boreal and temperate montane-subalpine coniferous) and *Betulo-Alnetea viridis* (subarctic-subalpine deciduous) (Figure 1). Azonal forests can be arranged into two groups: *Erico-Pinetea*, *Pyrolo-Pinetea* and *Junipero-Pinetea* include coniferous forests on very dry sites, while *Salicetea purpureae*, *Alno-Populetea* and *Alnetea glutinosae* are wetland forests. Finally, the *Crataego-Prunetea*, *Franguletea* and *Robinietea*

comprise seral woodland and tall-scrub (Mucina et al. 2016). These classes can be incorporated into a global formation system, enabling broad-scale comparisons among continents (Willner and Faber-Langendoen 2021).

For most of the 20th century, the correspondence between classes and formations was much weaker because some classes (*Vaccinio-Piceetea*, *Betulo-Adenostyletea*, *Epilobietea*) included both forest and non-forest vegetation (e.g., Oberdorfer 1957). Splitting these physiognomically heterogeneous classes has been identified as one of the megatrends in phytosociology during the last 50 years (Guarino et al. 2018; Willner and Faber-Langendoen 2021). However, many uncertainties and inconsistencies still linger within the classes, blurring the biogeographical and ecological correspondences outlined above. For instance, the EuroVegChecklist (EVC, Mucina et al. 2016) classifies Western Caucasian *Pinus brutia* forests (*Campanulo sibiricae-Pinion brutiae*) in the *Quercetea pubescentis* while the *Pinus brutia* forests of the Eastern Mediterranean are included in the *Quercetea ilicis* (but see Bonari et al. 2021 for a different solution). Boreal-subarctic birch woods on nutrient-poor podzolic soils (*Empetro hermaphroditi-Betulion pumilae*) are included in the *Vaccinio-Piceetea*, those on nutrient-rich soils (*Geranio sylvatici-Betulion pumilae*) in the *Betulo-Alnetea viridis*. Temperate pine forests on acidic soils (*Dicrano-Pinion sylvestris*) are classified within the *Vaccinio-Piceetea* by the EVC, whereas Willner

and Grabherr (2007) assign them to the *Erico-Pinetea*. Acidophytic beech forests are placed in the *Carpino-Fagetea* by some authors, but in the *Quercetea robori-petraeae* by others (Willner 2002; see also remark *fag03* in Mucina et al. 2016, p. 35). High montane acidophytic beech forests of Central Europe (*Calamagrostio villosae-Fagetum*) were even assigned to the *Vaccinio-Piceetea* in Oberdorfer (1992). Temperate *Abies alba* forests are either considered as part of the *Carpino-Fagetea* (e.g., Chytrý 2013), or as part of the *Vaccinio-Piceetea* (e.g., Willner and Grabherr 2007; Mucina et al. 2016), whereas some authors split them between the two classes (Oberdorfer 1992).

All these examples have one question in common: Should one give higher weight to the tree layer or the herb layer composition when classifying forests? Floristic similarity is the main criterion in the Braun-Blanquet approach (Westhoff and Van der Maarel 1978). However, floristic similarity of the tree layer might suggest a different grouping than floristic similarity of the herb layer. As the European tree flora is rather poor in species compared to other continents (Leuschner and Ellenberg 2017), overall similarity is usually driven by the herb layer. Thus, following a purely floristic approach, communities dominated by the same tree species may end up in different classes, orders or alliances (Grabherr et al. 2003). Because such units are often very heterogeneous in terms of physiognomy and at odds with broad-scale formations and biogeographical

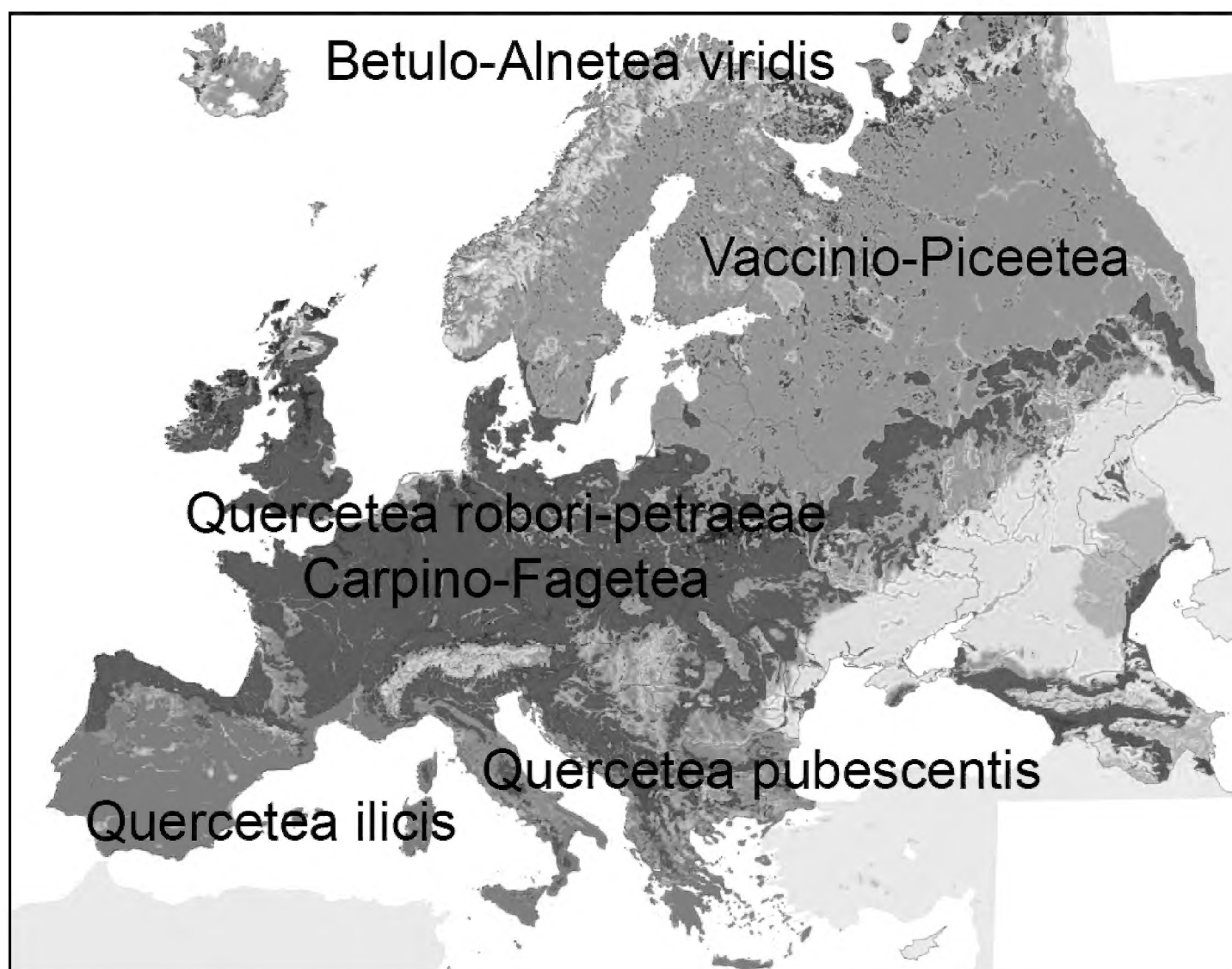


Figure 1. Main zonal formations of Europe (following Bohn et al. 2000) and corresponding EVC classes. Orange: mediterranean sclerophyllous forests and scrub (*Quercetea ilicis*); yellow-green: submediterranean deciduous broad-leaved forests (*Quercetea pubescentis*); dark green: cool-temperate deciduous broad-leaved forests (*Quercetea robori-petraeae*, *Carpino-Fagetea*); lilac: boreal, hemiboreal and temperate-montane coniferous and mixed broad-leaved-coniferous forests (*Vaccinio-Piceetea*); pale pink: subarctic and temperate-subalpine open woodland and scrub (*Betulo-Alnetea viridis*).

units, most authors consciously or unconsciously give higher weight to the tree species composition in at least some cases. However, in the absence of a general rule, these decisions are mostly subjective and arbitrary, resulting in a low stability of the forest classification in Europe.

Similar problems arise from the shrub layer, especially for communities without a tree layer. In the past, shrub communities were either joined with forests or with herb vegetation: The *Prunetalia spinosae* were part of the *Quercus-Fagetum*, the *Sambucetalia racemosae* part of the *Epilobietum angustifolii*, the *Betulo-Alnetum viridis* included in the *Betulo-Adenostyletum* etc. (Oberdorfer 1992; Mucina et al. 1993). Whether shrub communities should be separated from forests on a high syntaxonomic level is still a controversial issue (e.g., Loidi 2020). Indeed, while the classes *Crataego-Prunetum* and *Betulo-Alnetum viridis* have been widely accepted in recent decades, they still include communities dominated by either shrubs or trees (see Mucina et al. 2016). The distinction between trees and tall shrubs is not always straightforward as many woody species have a rather high phenotypic plasticity. For instance, *Fagus sylvatica* often has a prostrate growth form at its upper elevational limit (Willner 2002), *Quercus pubescens* may be less than 4 m tall on dry sites with shallow soils (Jakucs 1961), while *Corylus avellana* can achieve 10 m in height despite having a shrubby branching pattern (Schütt and Lang 2014). Therefore, *a priori* separation of forests and tall scrub is inevitably at odds with the floristic principle (see also Willner and Faber-Langendoen 2021).

Interestingly, the traditional classification of tall shrub vegetation is almost exclusively based on the species composition of the shrub layer (Tüxen 1952; Weber 1997; Willner and Grabherr 2007). Herbs and grasses are often confined to the fringes and gaps of the scrub while the dense interior is almost completely devoid of a herb layer (Weber 1999). Therefore, non-woody species in relevés mainly reflect the neighbouring fringe and grassland vegetation, which belongs to a different successional stage, and their presence is strongly dependent on the delimitation of the sampling plot. Since the classification of scrub communities should reflect the ecological and biogeographical properties of the dominant shrubs rather than those of adjacent herbs and grasses, it makes sense to ignore the latter in the delimitation of higher syntaxa.

In an effort to increase the consistency of the Central European forest classification, Willner and Grabherr (2007) adopted an approach for the definition of higher forest syntaxa that was similar to that of tall shrub vegetation; that is, they suggested that the upper units of the system should be primarily based on the species composition of the tree layer, whereas the lower ones should be primarily based on the understorey composition (Willner 2017). Depending on the ecological amplitude of the dominant trees, the switch between over- and understorey was done at different hierarchical levels (e.g., between order and alliance for spruce forests, and between alliance and suballiance for most deciduous forests). However, the principle was not rigorously applied using numerical methods.

In the present study, I investigate whether a classification of Central European forests based solely on the woody species of the shrub and tree layer leads to units similar to the traditional Braun-Blanquet system or to something completely different.

Study area

The plot records (relevés) used in this study are from Austria (Central Europe) and adjacent regions in the SE Alps and NW Dinaric mountains (Figure 2). Austria covers most of the Eastern Alps and their foreland, the western part of the Pannonian Basin and the SE part of the Bohemian Massif. The elevation of the plots ranges from 120 m a.s.l. in Eastern Austria to the highest forests in the Alps at ca. 2300 m a.s.l. Annual precipitation ranges from 500 mm to 2000 mm (in the SE Alps locally up to 3000 mm). The mean annual temperature ranges from 1–2°C at the treeline to 10°C in the Pannonian lowland.

Due to the large climatic gradient Austria has a large variety of forest types, and forests cover 46% of the country (ca. 3.88 million hectares). Lowland forests are mostly deciduous, and oaks (*Quercus* spp.), hornbeam (*Carpinus betulus*), beech (*Fagus sylvatica*) and ash (*Fraxinus excelsior*) are dominant trees. The outer ranges of the Alps are occupied by mixed forests composed predominantly of beech and fir (*Abies alba*). The inner parts of the Alps, which have a strongly continental climate, and the whole subalpine belt are covered by coniferous forests with spruce (*Picea abies*), larch (*Larix decidua*), and Arolla pine (*Pinus cembra*) as dominants. The upper subalpine belt is often dominated by *Pinus mugo* krummholz (Mayer 1974).

Methods

Dataset preparation

Initially, all relevés of forest and shrub communities were selected from the Austrian Vegetation Database (GIVD-ID EU-AT-001; Willner et al. 2012). Spruce and pine plantations and stands with a cover of non-native woody species > 5% were excluded from the dataset. Also excluded were forest relevés where the cover of trees was not estimated separately for the tree and herb layer, relevés with a cover of woody species determined only at the genus level > 5%, and relevés dominated by (>25%) low shrubs [i.e., shrub species not exceeding 2 m, including all *Rubus* species]. The 2 m threshold was chosen following the definition of the forest and woodland formation class (Willner and Faber-Langendoen 2021). Finally, relevés with a total cover of trees and tall shrubs < 15% were omitted. This resulted in a dataset of 23,681 relevés, with 22,588 plots from Austria and 1,093 plots from neighbouring countries (Figure 2).

Only native tree and tall shrub species in the shrub and tree layer were used in the classification while all other taxa (including records of woody species in the herb layer and

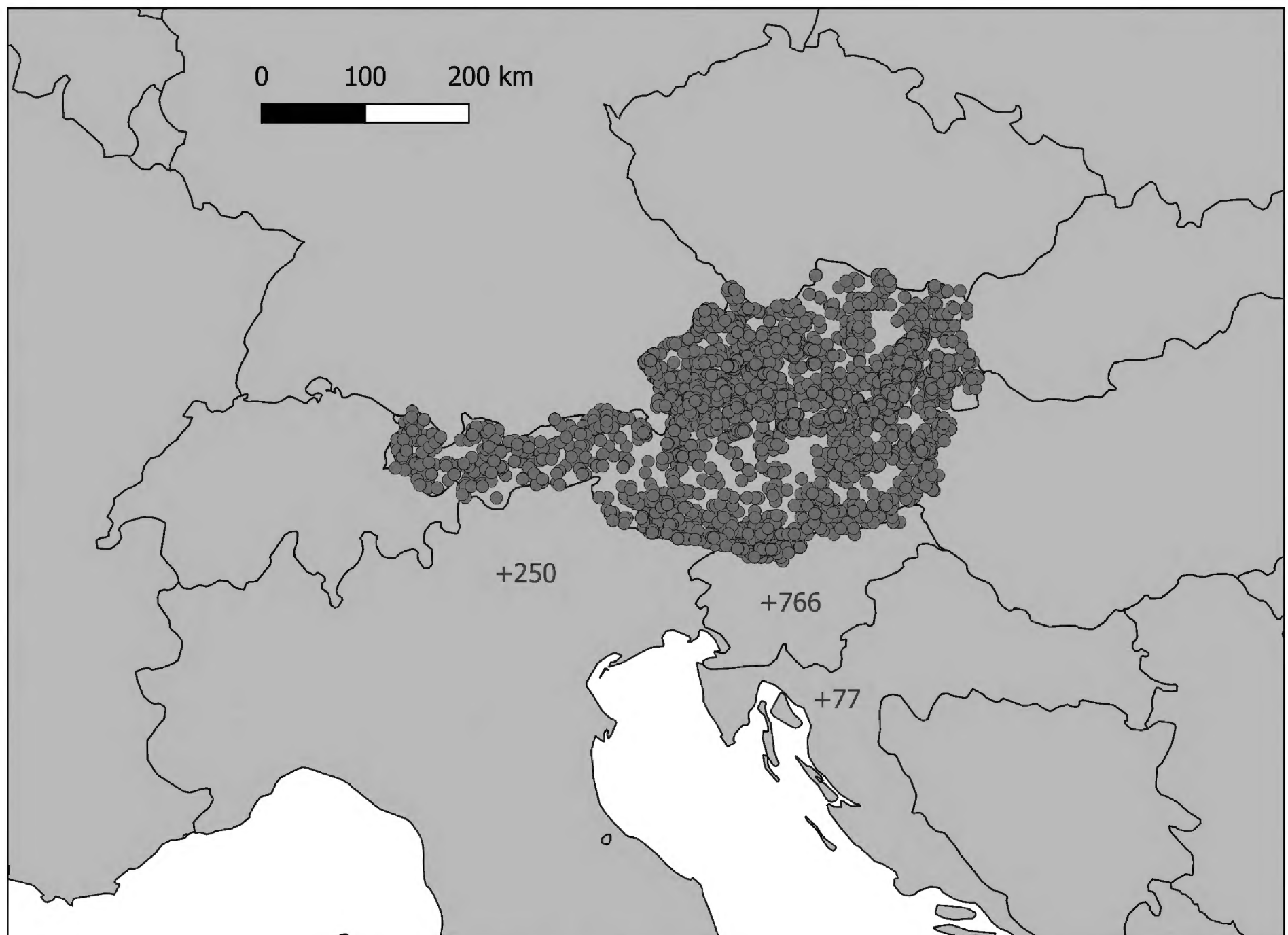


Figure 2. Plot locations in Austria (green dots) and adjacent areas (green numbers, indicating the number of plots from northern Italy, Slovenia, and Croatia, respectively).

taxa determined only at the genus level) were omitted. The omission of non-native trees and shrubs follows the consideration that the syntaxonomic system of European forest and shrub communities should be based on the native species (though syntaxa for communities dominated by non-native species might be added in a second step). Records of native tree and tall shrub species in different layers were merged using the algorithm published by Fischer (2015). Altogether, 111 taxa were kept in the final dataset. All data handling was done with JUICE 7.1 (Tichý 2002).

Numerical classification

The matrix of 23,681 relevés and 111 taxa was classified using the original TWINSpan algorithm (Hill 1979). Parameter settings were three pseudospecies cutlevels (0%, 5%, 25%), six levels of division and a minimum group size for division of two. For species sorting and interpretation, the diagnostic value of woody species for phytosociological classes according to Mucina et al. (2016) was used. If a species was given as diagnostic for two or more classes occurring in Central Europe, the diagnostic value according to Willner and Grabherr (2007) was followed. Within each class, species were sorted by decreasing phi coefficient (Chytrý et al. 2002; Tichý and Chytrý 2006) using a threshold of 0.3. The phi coefficient was

calculated assuming equal group size, and positive phi values were only accepted if the difference in species constancy between the target unit and the rest of the data set was significant according to Fisher's exact test at $p < 0.05$.

Results

The TWINSpan classification resulted in 63 clusters (one division failed because the minimum group size was not reached). With a few exceptions, lowland forests and scrubs were separated from those at higher elevations at the first level of division. At the second division level, lowland communities were further divided along a moisture gradient, and montane communities were separated from subalpine ones (Table 1).

Specifically, the TWINSpan clusters corresponded to the following vegetation types (numbers in brackets refer to the column number in Table 1 and Suppl. material 1, syntaxa follow the EVC system; the clusters are numbered from 1 to 64 to show the full TWINSpan hierarchy; note that there is no cluster 48 because the corresponding level 6 division failed):

1–8 (1): nutrient-rich willow carrs with *Salix cinerea* (*Salicion cinereae* p.p.)

- 9–12 (2): submontane and montane alluvial willow scrub (*Salicion eleagno-daphnoidis*)
13 (3): alluvial forests with *Salix alba* (*Salicion albae* p.p.)
14 (4): alluvial forests with *Salix fragilis* (*Salicion albae* p.p.)
15–16 (5): lowland alluvial scrub with *Salix triandra* (*Salicion triandrae*)
17–20 (6): swamp forests with *Alnus glutinosa* (*Alnion glutinosae*)
21 (7): alluvial forests with *Populus alba* (*Alnion incanae* p.p.)
22 (8): alluvial forests with *Alnus incana* (*Alnion incanae* p.p.)
23 (9): alluvial forests with *Alnus glutinosa* (*Alnion incanae* p.p.)
24 (10): sycamore forests (*Tilio-Acerion*)
25 (11): moist oak-hornbeam forests with *Quercus robur* (*Carpinion betuli* p.p.)
26 (12): lime forests and mesic oak-hornbeam forests with *Fraxinus excelsior* (*Melico-Tilion platyphylli*, *Carpinion betuli* p.p.)
27 (13): mesic and dry oak-hornbeam forests with *Quercus petraea* (*Carpinion betuli* p.p.)
28 (14): acidophytic oak forests with *Quercus petraea* (*Agrostio-Quercion petraeae*)
29 (15): thermophilous oak forests on deeper soils (*Quercion petraeae*, *Quercion pubescenti-petraeae* p.p.)
30 (16): thermophilous oak forests on shallow soils with *Quercus pubescens* (*Quercion pubescenti-petraeae* p.p.)
31 (17): thermophilous seral scrub (*Berberidion vulgaris*, *Urtico-Crataegion*)
32 (18): lowland alluvial hardwood forests (*Fraxino-Quercion roboris*)
33–36 (19): beech forests (*Fagetalia sylvaticae*, *Luzulo-Fagetalia sylvaticae*)
37–38 (20): spruce forests (*Piceetalia excelsae*, *Athyrio filicis-feminae-Piceetalia*)
39–40 (21): montane elder scrub in forest clearings (*Sambuco-Salicion capreae*)
41 (22): *Pinus sylvestris* forests (*Erico carnea-Pinion*, *Dicrano-Pinion sylvestris*, *Vaccinio uliginosi-Pinion sylvestris*)
42 (23): *Pinus nigra* forests (*Erico-Fraxinion orni*)
43–44 (24): dry calcareous *Ostrya carpinifolia* forests on shallow soils (*Fraxino orni-Ostryion*)
45–47 (25): nutrient-poor willow carrs with *Salix aurita* (*Salicion cinereae* p.p.)
49–52 (26): subalpine krummholz with *Pinus mugo* (*Pinion mugo*, *Erico-Pinion mugo*)
53–54 (27): subalpine *Larix decidua* woodland (*Piceion excelsae* p.p.)
55–56 (28): subalpine *Pinus cembra* woodland (*Piceion excelsae* p.p.)
57–64 (29): subalpine green alder scrub (*Alnion viridis*)

Discussion

Syntaxonomy

The TWINSpan classification revealed elevation (i.e., climate) as the main floristic gradient in the data set. Within

lowland communities, soil moisture was the dominant factor. Interestingly, the higher units of the Braun-Blanquet system were mostly well reproduced, with clusters 1–8 corresponding to the *Franguletea*, clusters 9–16 to the *Salicetea purpureae*, clusters 17–20 to the *Alnetea glutinosae*, clusters 21–23 to the *Alno-Populetea*, clusters 24–27 to the *Carpino-Fagetea* and so on. Notable exceptions are the classes *Quercetea pubescentis*, *Quercetea robori-petraeae* and *Crataego-Prunetea*, which were all intermingled with the *Carpino-Fagetea*. This could be interpreted as support for the more traditional concept of a broadly defined class *Quercu-Fagetea* (e.g., Oberdorfer 1992; Loidi 2020). However, because the *Quercetea pubescentis* and *Quercetea robori-petraeae* have their main distribution outside the study area, this question will not be further discussed in the present paper. The strange position of the *Fraxino orni-Ostryion* in the TWINSpan table reflects the fact that *Ostrya carpinifolia* forests reach their northern distribution limit in the study area, where they are confined to dry, calcareous sites similar to those of pine forests. Indeed, Mucina et al. (1993) classified these communities within the class *Erico-Pinetea*. Alluvial hardwood forests (*Fraxino-Quercion roboris*) were widely separated from the *Alnus* and *Populus* woods of the *Alnion incanae*, which suggests keeping them in the class *Carpino-Fagetea*. Lime forests (*Melico-Tilion platyphylli*) were grouped together with oak-hornbeam forests (*Carpinion betuli*). *Abies alba* forests were not reproduced as a separate cluster, but mostly included in beech forests, supporting the concept of Chytrý (2013). The position of subalpine *Larix decidua* and *Pinus cembra* woodland seems at odds with the EVC system, but it fits well with the classification in Willner and Grabherr (2007), where both units were included in a broadly defined *Pinion mugo*.

On the whole, the traditional Braun-Blanquet system of forests seems to have given more weight to the tree species combination than is generally acknowledged in textbooks. As expected, the syntaxonomic rank of the TWINSpan clusters varies vastly, from a single association (e.g., cluster 13: *Salicetum albae*) to a group of classes (cluster 41: *Pinus sylvestris* forests). This reflects the different ecological amplitude of the dominant species. In most cases, however, the woody species combination seems most suitable for the definition of orders and alliances. Some ecological gradients (e.g., calcareous versus acidic soils) are only visible in the herb layer (including dwarf shrubs) and are therefore not reflected in the table.

What do we expect from a good forest classification?

Loidi (2020) suggested three criteria for a “good” phytosociological class: (1) biogeographical-evolutionary criterion: common origin and evolution, (2) floristic criterion: common set of characteristic species, and (3) application criterion: coherence in the presentation. For

Table 1. Synoptic table of the TWINSPAN result. Values are percentage constancy. Bold values indicate an average cover > 14%, grey shading indicates high fidelity (i.e., phi > 0.3). Species are sorted according to their diagnostic value for classes. The vertical lines represent the division level 2. Groups 21 and 25 (with 14 and 10 relevés, respectively) and species not reaching 10% constancy in any column are omitted. The full table is provided in Suppl. material 1.

Group number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	22	23	24	26	27	28	29
TWINSpan level	3	4	6	6	5	4	6	6	6	6	6	6	6	6	6	6	6	6	4	5	6	6	5	4	6	6	3
Number of relevés	121	307	318	110	109	855	250	833	1087	1013	393	1847	653	397	749	546	299	96	5232	5090	1181	255	327	1000	149	133	307
Franguletea	95	1	3	3	4	14	1	3	2	1	1	1	.	.	1	1	.	.	1	.	.	.
<i>Salix cinerea</i>																											
Salicetea purpureae	.	57	4	9	3	.	1	5	3	5	.	1	.	.	1	1	1	.	1	1	3	1	3	1	.	.	1
<i>Salix eleagnos</i>	.	17	1	1
<i>Myricaria germanica</i>	.	21	5	.	1	1	1	6	1	1	1	.	.	1	1	.	.	1	.	.	1
<i>Salix myrsinifolia</i>	.	15	3	.	2	.	.	2	1	1	1	.	.	.	1	.	.	1
<i>Salix daphnoides</i>	19	6	20	91	9	9	2	3	12	1	1	1	1
<i>Salix fragilis</i>	1	1	2	24	6	2	1	.	1	.	1
<i>Salix x rubens</i>	1	10	14	30	92	1	.	1	1	1
<i>Salix triandra</i>	.	3	8	14	39	1	.	1	1	1	.	1	1
<i>Salix viminalis</i>	1	82	31	57	33	1	2	6	6	1	1	1	.	1	1	.	1	6	.	1	1	.	.	1	.	.	.
<i>Salix purpurea</i>	5	16	97	32	62	2	25	8	7	1	1	1	.	1	1	.	1	2	1	.	1
<i>Salix alba</i>																											
Alnetea glutinosae	27	2	4	34	3	99	9	2	50	7	10	5	1	1	1	.	1	5	1	1	1	.	.	1	.	.	.
<i>Alnus glutinosa</i>	9	4	3	1	.	30	6	8	8	3	22	4	1	23	8	4	4	18	3	4	17	2	1	3	.	.	.
<i>Frangula alnus</i>																											
Alno-Populetea albae	.	18	36	12	6	1	22	5	4	1	1	1	1	.	1	.	1	7	1
<i>Populus nigra</i>	1	1	4	.	1	2	62	3	7	1	2	1	1	1	2	1	1	33	1	1
<i>Populus alba</i>	2	43	39	35	4	4	46	99	24	26	2	1	.	1	1	.	.	.	1	6	2	.	1	1	.	3	2
<i>Alnus incana</i>	4	6	27	17	.	36	50	40	72	11	8	7	1	1	4	1	3	7	1	1	1	.	.	1	.	.	.
<i>Prunus padus</i>	.	.	3	.	.	1	14	1	3	1	12	3	1	1	19	4	16	70	1
<i>Ulmus minor</i>	1	.	1	1	1	2	6	1	1	.	11	1	1	.	1	.	.	32
<i>Fraxinus angustifolia</i>	7	4	17	9	1	17	18	15	25	7	7	6	1	2	5	1	5	8	1	1	1	1
<i>Viburnum opulus</i>	.	.	9	8	.	1	30	2	9	1	4	2	1	.	1	.	1	24	1	1
<i>Ulmus laevis</i>																											
Crataego-Prunetea	2	5	36	18	3	7	90	31	48	11	22	22	4	13	51	44	44	78	1	1	2	2	1
<i>Cornus sanguinea</i>	1	1	4	1	.	4	15	6	16	1	12	13	12	18	76	53	60	45	1	1	7	4	4
<i>Ligustrum vulgare</i>	.	1	2	1	.	1	2	6	9	7	3	14	2	2	43	53	22	2	1	1	12	5	10	1	.	.	.
<i>Viburnum lantana</i>	1	.	1	.	.	1	5	1	1	1	7	1	1	5	18	12	68	21	1	.	1	1
<i>Prunus spinosa</i>	1	1	1	1	.	1	8	1	3	1	4	3	4	9	24	29	77	17	1	1	1	4	1
<i>Rosa canina</i> agg.	.	1	.	.	.	1	.	1	.	1	2	1	1	4	5	8	4	.	1	2	53	7	7	3	.	1	1
<i>Juniperus communis</i>	1	1	2	1	.	1	33	.	.	1	1	41	70	30	6	.	.	.
<i>Amelanchier ovalis</i>	1	.	.	.	6	.	.	1	1	7	25	15	1	.	.	.
<i>Cotoneaster tomentosus</i>	1	2	6	1	2	2	30	12	17	5	22	22	12	17	73	68	74	64	1	1	4	8	4
<i>Crataegus monogyna</i>	.	2	3	3	.	5	3	9	49	62	55	49	9	40	30	29	9	23	11	4	9	5	8	1	.	.	1
<i>Corylus avellana</i>	.	1	3	.	.	3	3	10	6	6	5	7	1	7	17	47	11	.	2	2	34	47	9	1	.	.	.
<i>Berberis vulgaris</i>	2	1	10	9	1	13	27	19	33	6	12	12	3	2	25	12	37	18	1	1	1	.	1
<i>Euonymus europaeus</i>	.	.	1	1	.	9	3	1	2	1	5	5	2	3	14	35	30	19	1	1	3	3	3
<i>Rhamnus cathartica</i>	1	.	.	1	13	7	.	.	.	1	1
<i>Prunus mahaleb</i>	1	.	.	1	13	7	.	.	.	1	1
Quercetea pubescentis	1	1	1	.	1
<i>Quercus cerris</i>	1	3	5	28	11	48	9	6	3	1	1
<i>Quercus pubescens</i>	1	2	1	.	26	76	4	1	1	.	1	6	3
<i>Cornus mas</i>	1	.	1	1	3	16	9	1	39	64	3	3	1	1	.	9



Group number		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	22	23	24	26	27	28	29			
TWINSPAN level		3	4	6	6	5	4	6	6	6	6	6	6	6	6	6	6	6	6	4	5	6	6	5	4	6	6	3			
Number of relevés		121	307	318	110	109	855	250	833	1087	1013	393	1847	653	397	749	546	299	96	5232	5090	1181	255	327	1000	149	133	307			
<i>Euonymus verrucosus</i> <i>Ostrya carpinifolia</i> <i>Fraxinus ornus</i> <i>Sorbus aria</i> agg. <i>Sorbus torminalis</i> <i>Pyrus pyraister</i>		1	1	1	2	10	3	2	20	38	2	2	1	.	1	.	3			
		1	.	.	2	3	.	.	3	1	1	4	98	1	.	.	.			
		1	1	1	.	.	1	1	1	.	3	4	.	.	2	1	3	13	83	.	.	.			
		1	.	.	1	1	1	2	14	7	6	9	63	1	.	11	3	30	69	55	6	1	.			
		1	1	.	2	5	16	11	27	25	2	.	2	1	.	3			
		.	1	1	.	1	1	1	5	2	4	9	15	15	1	9	1	1	1	1	1		
		Quercetea roboris <i>Quercus robur</i> <i>Quercus petraea</i>		1	1	1	5	.	9	10	2	23	4	88	22	4	11	30	7	13	63	3	1	5	.	3	
				1	.	.	.	1	9	24	87	95	54	11	1	.	11	1	5	1	6	
				Carpino-Fagetea <i>Ulmus glabra</i> <i>Acer pseudoplatanus</i> <i>Acer platanoides</i> <i>Tilia platyphyllos</i> <i>Acer campestre</i> <i>Fagus sylvatica</i> <i>Fraxinus excelsior</i> <i>Carpinus betulus</i> <i>Lonicera xylosteum</i> <i>Tilia cordata</i> <i>Prunus avium</i> <i>Crataegus laevigata</i> <i>Staphylea pinnata</i> <i>Populus tremula</i>		.	3	1	5	.	1	3	3	17	60	2	34	2	1	5	5	1	1	10	1	1
						.	6	2	1	.	6	2	18	49	89	13	59	4	2	9	9	3	4	4	45	10	9	7	6	12	9
.	1	1	.			.	1	.	1	4	6	1	29	3	1	5	9	1	2	2	3	1	1	1	1		
.	.	1	.			.	1	.	1	2	10	2	30	6	5	5	18	1	1	.	2	1	1	2	2		
.	.	1	.			.	1	8	1	9	3	24	34	34	4	53	34	17	58	2	2	1	1			
.	1	.	.			.	2	.	1	5	39	15	61	46	16	5	17	.	.	.	97	21	9	25	29	5	2	.	1		
Vaccinio-Piceetea <i>Abies alba</i> <i>Picea abies</i> <i>Larix decidua</i> <i>Pinus cembra</i> <i>Pinus uncinata</i> <i>Lonicera caerulea</i>		1	10	9	16	.	35	43	39	91	88	17	74	13	3	45	57	9	21	16	1	2	7	1	1	.	.	.			
		.	1	1	1	.	5	1	1	16	9	64	69	92	54	36	18	3	16	6	6	1	1	.	2	.	.	.			
		.	7	7	3	1	2	9	21	34	25	8	24	4	3	26	15	4	4	5	5	2	10	1	5	1	1	.	1		
		.	.	1	1	.	1	2	1	12	8	29	37	32	23	15	13	1	1	5	2	1	1	1	2		
		.	1	1	1	.	1	1	2	8	5	23	24	17	17	28	9	20	5	3	3	1	1		
		1	.	1	2	1	9	12	11	4	19	14	2	14	1	1	1	1		
		1	3	1	13	2	.	4	14	1	.	.	1		
		.	1	1	.	.	.	1	1	1	3	2	20	3	2	8	2	1	3	8	1	1	2	1	2	.	1	.	1		
		Robinietea <i>Sambucus nigra</i>		1	.	1	2	8	3	7	3	2	1	1	.	.	50	26	1	1	1	1	5	7	.	1
				.	11	1	1	.	23	1	28	17	51	34	21	9	14	6	4	1	1	.	69	99	62	26	38	34	60	60	43
.	1			.	.	.	1	.	1	1	1	3	2	2	4	1	1	.	.	.	15	48	17	2	11	23	99	61	29		
.	1	7	1	.	.	3	51	100	11		
.	1	1	11	.	.	2	1	.	.		
.	1	.	1	1	1	1	1	.	1	6	11	3	5		
Erico-Pinetea <i>Pinus sylvestris</i> <i>Pinus nigra</i> <i>Rhamnus fallax</i>		3	6	40	45	2	15	46	41	62	45	12	18	3	2	13	1	30	13	4	1	1			
			
		2	5	1	.	.	.	3	.	2	1	1	20	5	8	52	12	8	1	1	12	15	93	23	42	1	.	1	.		
		2	2	1	2	34	2	.	2	1	3	98	10		
Roso pendulinae-Pinetea mugo <i>Sorbus chamaemespilus</i> <i>Pinus mugo</i> (s. str.) <i>Rosa pendulina</i>		1	1	6	.	.	22	25	2	2			
		.	1	.	.	.	1	1	1	4	11	1	5	98	72	29	7		
		1	.	1	1	2	.	1	1	.	.	.	1	.	.	2	2	3	2	1	16	15	.	1		
		Betulo-Alnetea viridis <i>Alnus alnobetula</i> <i>Salix appendiculata</i>		.	.	.	1	.	1	.	1	1	3	1	.	1	9	24	13	96	
.	13			1	.	.	1	.	3	1	5	1	1	1	.	.	1	.	1	.	1	3	2	1	2	23	16	2	24		
other species <i>Sorbus aucuparia</i> <i>Betula pendula</i>				1	1	1	1	.	8	.	5	7	5	13	6	2	8	2	1	1	1	8	21	15	2	4	34	64	23	47	
				.	7	3	6	.	2	2	4	4	2	25	6	14	25	3	1	2	2	4	4	7	7	1	2	1	3	3	14

the third criterion, he noted that “it is very difficult to argue, in a teaching context, that forests dominated by the same species belong to different classes”. Obviously, the second and third criterion can only be simultaneously fulfilled if the class is floristically defined by the species of the dominant layer. In this way, most European tree species become character species on some hierarchical level while in many traditional systems they are only treated as companion species.

We might complement Loidi’s criteria by four general properties that users might reasonably expect from a good forest classification: (a) The upper levels of the hierarchy are more easily recognizable than the lower levels. (b) The upper level units are more stable over time in terms of vegetation history. (c) The factors shaping global vegetation patterns are reflected on the upper levels, while the factors responsible for regional and local patterns are reflected on the lower levels. (d) The upper levels are consistent with global formation and biome classifications.

As shown above, the higher levels of the phytosociological forest system can basically be defined by taking only the tall shrub and tree layer into account. However, this has never been formulated as a rule, and all past and current classifications suffer from arbitrary weighting of the layers, leading to inconsistencies and blurring the main biogeographical patterns within European forests. The distribution of European tree species is mainly controlled by broad climatic gradients as well as differences in soil moisture (Table 1) – the same ecological factors that are reflected in global biome and formation systems (Walter 1976; Faber-Langendoen et al. 2016; Loidi et al. 2022). Differences in calcium content, on the other hand, have a more regional significance, and are mostly visible in the herb layer composition (Leuschner and Ellenberg 2017). It is therefore advisable to reflect the latter on lower hierarchical levels, e.g., by uniting basiphytic and acidophytic beech forests in the same class or even order (Moor 1978; Oberdorfer 1992; Willner and Grabherr 2007; Willner et al. 2017), or by transferring temperate dry *Pinus sylvestris* forests on acidic bedrock (alliance *Dicrano-Pinion*) from the *Vaccinio-Piceetea* to the *Erico-Pinetea* – a solution that is also supported by numerous common understorey species (Willner and Grabherr 2007). However, given the extremely broad amplitude of *Pinus sylvestris*, it is also justified to classify the forests dominated by this species in at least two different classes, *Erico-Pinetea* (temperate dry pine forests, including the *Erico-Pinion*, *Dicrano-Pinion*, *Ononido-Pinion* and other alliances) and *Vaccinio uliginosi-Pinetea* (boreal and temperate wet pine forests, including the *Vaccinio uliginosi-Pinion* and *Cladonio stellaris-Pinion*; see Ermakov and Morozova 2011). Submediterranean pine forests dominated by *Pinus nigra* should probably be placed in a separate class.

Understorey species may have markedly different biogeographical histories than the tree species they are currently associated with (Záveská et al. 2021; Willner

et al. 2023). Thus, we can assume that vegetation units defined by tree species have been more stable over time than syntaxa defined by species from different layers. In fact, vegetation units solely defined by understorey species can be completely independent of the tree layer and even exist outside the forest. A classic example is Braun-Blanquet’s *Rhododendro-Vaccinion* (Braun-Blanquet et al. 1939), which comprised both coniferous forests and treeless dwarf shrub heaths. Carrying this idea to extremes, Gillet (1988) proposed to independently classify the herb, shrub and tree layers (see also Gillet and Julve 2018). While agreeing with these authors on the basic problem, I suggest a different and less radical solution: By using the tree and (tall-)shrub layer for defining the upper levels and the herb and cryptogam layer for defining the lower levels of the system, the basic units (i.e., the associations) represent the whole forest community. At the same time, over- and understorey composition are not mixed in an arbitrary and often confusing manner for the definition of the higher units as in most traditional systems. However, it must be emphasised that “upper” and “lower” level is meant in a purely relative sense here. The lowest appropriate rank to be defined by the tree and tall shrub layer depends both on the ecological amplitude of the resulting units and the floristic heterogeneity of the herb and cryptogam layer within these units; thus, it may vary from association or suballiance (though this will be uncommon) to a group of classes (see examples above).

Previous proposals have suggested separating forests and tall-scrub on the one hand and non-woody vegetation (including dwarf-shrub heaths) on the other hand as two *a-priori* structural types in syntaxonomy (Bergmeier et al. 1990; Dengler et al. 2005). If trees and tall-shrubs are used to define the classes of woody vegetation, this separation becomes a natural component of the floristic classification, without a sudden change of criteria. At the same time, phytosociological classes defined by the combination of woody species can be easily fitted into a global formation system (Willner and Faber-Langendoen 2021) as well as in most biome systems (Mucina 2019; Keith et al. 2022).

Data availability

The relevés used in this study are available upon request from the Austrian Vegetation Database (GIVD-ID EU-AT-001) managed by the author of this paper and from the European Vegetation Archive (<https://euroveg.org/eva-database/>).

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Supplementary material

Supplementary material 1

Full synoptic table

Link: <https://doi.org/10.3897/VCS.117703.suppl1>